

Retinotopic sensitisation to spatial scale: Evidence for flexible spatial frequency processing in scene perception

Emre Ozgen^{a,b,*}, Helen E. Payne^b, Paul T. Sowden^b, Philippe G. Schyns^c

^a Department of Psychology, Bilkent University, Bilkent, Ankara 06800, Turkey

^b Department of Psychology, University of Surrey, Guildford, Surrey GU2 7XH, UK

^c Department of Psychology, University of Glasgow, 58 Hillhead Street, Glasgow G12 8QB, UK

Received 1 June 2005

Abstract

Observers can use spatial scale information flexibly depending on categorisation task and on their prior sensitisation. Here, we explore whether attentional modulation of spatial frequency processing at early stages of visual analysis may be responsible. In three experiments, we find that observers' perception of spatial frequency (SF) band-limited scene stimuli is determined by the SF content of images previously experienced at that location during a sensitisation phase. We conclude that these findings are consistent with the involvement of relatively early, retinotopically mapped, stages of visual analysis, supporting the attentional modulation of spatial frequency channels account of sensitisation effects.

© 2005 Elsevier Ltd. All rights reserved.

Keywords: Spatial frequency; Scene perception; Retinotopic specificity; Hybrid; Channel; Attention; Attentional modulation

1. Introduction

Evidence has been accumulating for some time suggesting that processing of spatial scale might be influenced by a variety of task-dependent factors such as type of categorisation (Schyns & Oliva, 1999; Schyns, Bonnar, & Gosselin, 2002), sensitisation through repeated exposure to spatial frequency filtered scenes (Oliva & Schyns, 1997), and attention (Özgen, Sowden, Schyns, & Daoutis, 2005; Sowden, Özgen, Schyns, & Daoutis, 2003). For example, Schyns and Oliva (1999) used “hybrid” face stimuli, which contained both a low-pass (LSF) and a high-pass (HSF) spatial frequency (SF) filtered face in the same image. They found that observers reported seeing only one of the two components of a hybrid face, which depended on the type of face categorisation they

were asked to carry out—i.e., they reported seeing the HSF face when judging if a face was expressive or not, and the LSF face when categorizing expressions. In a related vein, Oliva and Schyns (1997) repeatedly presented observers with scenes of one type of SF content (either LSF or HSF) combined with noise on the opposite scale, and asked observers to categorise them as “city” or “highway”. Subsequently, and unknown to the observers, hybrid scenes were displayed, where both an LSF-scene and an HSF-scene (one highway, one city) were present. Observers who were sensitised with LSF scenes reported seeing the LSF component (e.g., the highway), and those sensitised with HSF scenes reported seeing the HSF component of hybrids (e.g., the city), but not both.

1.1. Sensitisation and attentional modulation of spatial frequency processing

The precise mechanisms involved in these phenomena are open to study. We propose that sensitisation

* Corresponding author. Tel.: +90 312 2903415; fax: +90 312 2664960.

E-mail address: Eozgen@bilkent.edu.tr (E. Ozgen).

(resulting from categorisation, restriction of information to a region of the SF spectrum, or explicit top-down cueing) directs attention to those SF channels in early vision whose output is diagnostic for a given task. We found strong evidence that a top-down attentional process can sensitise observers to specific SF channels (Sowden et al., 2003). In one experiment, observers made left–right tilt judgments on sinusoidal gratings presented at threshold contrast. We created SF uncertainty (Davis & Graham, 1981; Davis, Kramer, & Graham, 1983; Hübner, 1996a, 1996b) by presenting gratings at one of two possible SF's (e.g., 0.5 and 8 cycles/deg) intermixed randomly, and trained observers to attend to a symbolic sound cue acting top-down (cf. Hübner, 1996a, 1996b), signalling the SF of each grating. Subsequently, we interleaved *plaid* stimuli, which consisted of two superimposed gratings (one at each SF) at opposite orientations, to draw an analogy to hybrids. On these trials observers typically reported the orientation of the plaid component corresponding to the cued SF and never perceived both components. In further experiments we found that these effects of expectancy on grating detection were selective for SF in a manner similar to the SF channel tuning observed at early stages of visual analysis. This effect of sensitising observers to SF using sound cues is analogous to the sensitisation to spatial scale, resulting from categorisation experience, reported by Schyns and Oliva (1999) and Schyns et al. (2002) where task cues the observer to attend to information at specific SF's. Making this link explicit Özgen et al. (2005) showed that sound cues can drive attention, top-down, to the spatial scale of scenes. In their experiments, during a sensitisation phase, observers made highway vs. city judgements on images combining a meaningful scene at one SF and noise at the opposite SF, presented at threshold contrast. Observers were trained to attend to a sound cue signalling the SF of the scene component of the image. In a subsequent, crucial, test phase, images containing meaningful scenes at the uncued SF and noise at the cued SF (invalid trials) were interleaved with sensitisation trials. Scene categorisation on these invalid trials was worse than when the cue was valid suggesting that cueing acted to focus attention to specific SF bands.

In sum, there is now considerable evidence that a similar process takes place in the perception of our hybrid scenes and gratings. Further, our work on grating discrimination and detection suggests that attention may modulate the activity of early SF channels resulting in the selective perception of these stimuli. Related to this work, Bonnar, Gosselin, and Schyns (2002) recently found evidence for bottom-up effects involving flexible use of spatial scale. They adapted observers to low-pass or high-pass dynamic noise presented over the entire display area, and subsequently presented them with an ambiguous image (Salvador Dalí's painting of *Slave*

Market with Disappearing Bust of Voltaire), which had different perceptions depending on whether the fine (HSF) or coarse (LSF) features were attended to. They found that adaptation with LSF noise resulted in the perception of the HSF features leading to the perception of the nuns in the ambiguous image and vice versa (i.e., adaptation with HSF noise resulted in the perception of the LSF features leading to the perception of Voltaire). It appears therefore that a bottom-up adaptation of SF channels forces observers to use the unadapted channels, and determines which scale information is perceived in the ambiguous image. However, the likely locus of this adaptation in the visual processing hierarchy has never been probed in detail. Thus, in the present work we directly explore whether the selective perception of complex stimuli such as hybrid images, like that of grating and plaid stimuli, can result from modulation of early visual processing.

1.2. The locus of sensitisation effects: Exploring retinotopic specificity

We address this issue by exploring the retinotopic specificity of the effects of sensitisation to spatial scale. At early stages of visual analysis, such as the primary visual cortex (V1), the visual field is retinotopically mapped in the brain (De Valois & De Valois, 1988; Tootell, Silverman, Switkes, & De Valois, 1982). Thus, if flexible scale use results from attentional modulation of SF channels at early stages of visual analysis, then it should be possible to sensitise observers (as in Oliva & Schyns, 1997—described above) to a different band of SF's at separate retinal locations. That is, flexible scale use should be retinal location specific at sufficiently fine resolutions to rule out the involvement of later stages of visual analysis such as the inferior temporal cortex.

The above possibility is supported by work on spatial attention, which has shown retinal location-specific enhanced stimulus processing. For instance, Posner (1980) reports that detection and discrimination are enhanced at cued locations in the visual field relative to uncued locations (see also Eckstein, Shimozaki, & Abbey, 2002 for an analysis of these effects). Spatial attention has also been shown to affect perceptual sensitivity at low-levels using signal detection paradigms (Bashinski & Bacharach, 1980; Hawkins et al., 1990), and vernier acuity tasks (Shiu & Pashler, 1995). Further, attention directed towards a specific location enhances spatial resolution at that location (Yesherun & Carrasco, 1999). Recently, it has been suggested that covert spatial attention operates on the basis of the specific cued retinal location (with the smallest tested separation at 2.3°), rather than an environmental reference point (Barrett, Bradshaw, Rose, Everatt, & Simpson, 2001). Spatial attention can be tuned to a very small area (Eriksen & Hoffman, 1972; LaBerge, 1983; Yantis, 1998) and this

location tuning can have an early locus (as early as 60 ms post-stimulus—Luck, 1998; Yantis & Johnston, 1990). These effects of spatial attention may reflect task-dependent modulation of early, retinotopically mapped, stages of visual analysis. There is now considerable evidence that spatial attention can modulate visual processing at stages as early as V1 and in other retinotopic visual areas (for recent reviews see Posner & Gilbert, 1999; Sengpiel & Hübener, 1999). Using fMRI, attention to cued locations has been found to modulate activity in V1 in a variety of tasks (Tootell et al., 1998; Gandhi, Heeger, & Boynton, 1999; Somers, Dale, Seiffert, & Tootell, 1999; Martinez et al., 2001). Similarly, recordings from single cells have revealed the involvement of V1, V2, and V4 in focal attention (Motter, 1993).

Perhaps closest to the approach taken here, previous research on perceptual learning has used retinotopic specificity as a marker for the involvement of early vision. A number of studies have found that improvement resulting from repeated practice on a variety of tasks such as pop out detection (Ahissar & Hochstein, 1996, 1997), vernier discrimination (Fahle, Edelman, & Poggio, 1995), and sinusoidal grating detection (Sowden, Rose, & Davies, 2002) fails to transfer to a different retinal location from the training location. Such positional specificity has been considered as evidence that V1 or other early stages of visual processing may be involved (Dill, 2002).

Here, we adopt a similar approach. In three experiments we tested retinotopic specificity of sensitisation effects using SF filtered scenes and hybrids. The idea common to these experiments is simple: we sensitised observers to low-pass or high-pass scenes at (a) particular location(s) in the visual field during a scene categorisation task. Subsequently, for Experiments 1 and 2, and unknown to the observer, we displayed hybrid images to test for transfer of sensitisation to different retinal locations. In Experiment 3, we replaced hybrid with incongruent trials. These incongruent trials, used to address a possible response bias explanation of Experiments 1 and 2, consisted of images containing a scene at the opposite scale to that to which the observer was sensitised for each location (plus noise at the sensitised scale). We examined category judgements in the hybrid (Experiments 1 and 2) and incongruent (Experiment 3) trials to indicate which scale participants attended to. Lack of transfer across retinal locations indicated retinotopic specificity of effects of sensitisation to spatial scale.

2. Experiment 1

In this experiment, we studied simple retinotopic specificity of effects of sensitisation to spatial scale, by testing transfer of sensitisation from one visual hemi-

field to another. Observers completed a sensitisation regime very similar to that reported by Oliva and Schyns (1997), except that opposite visual hemi-fields were sensitised to the opposite ends of the SF spectrum. Observers categorised a range of scenes as ‘highway’ or ‘city’. Computerised scene images were low- or high-pass filtered and combined with structured noise at the opposite scale, which meant that diagnostic information was restricted to only one end of the SF spectrum. In a sensitisation stage, observers categorised low- and high-pass scenes in opposite hemi-fields and, in a test stage, transfer of sensitisation to the opposite hemi-field was tested on hybrid images presented at each location. There were two transfer conditions: in the horizontal separation condition transfer across the vertical meridian between the *left* and *right* hemi-fields was tested, in the vertical separation condition transfer across the horizontal meridian between the *upper* and *lower* hemi-fields was tested. Vertical separation was tested to rule out possible hemisphere-specific sensitisation explanations. If sensitisation effects are retinal location specific, then sensitisation to low or high SF’s in a given hemi-field should fail to transfer to the opposite hemi-field. As a result, a hybrid image should be perceived orthogonally depending on which hemi-field it was displayed in.

2.1. Method

2.1.1. Observers

Twenty-six psychology undergraduates took part in the experiment. They all had normal or corrected to normal vision. They were paid a fee or offered course credits for their participation.

2.1.2. Stimuli and apparatus

Stimuli were constructed from a set of 80 highway and 80 city greyscale images. In addition, 64 structured noise patterns were created (described below). Two types of stimuli were constructed for “sensitisation” and “test” trials. Sensitisation stimuli (see Figs. 1A and B) comprised a low- or a high-pass scene combined with structured noise filtered in the opposite way to that of the scene (i.e., low-pass scene vs. high-pass noise or vice versa). Test stimuli (“hybrids”—see Fig. 1C) were a combination of a low-pass (low-spatial frequency—LSF) scene of one category and a high-pass (high-spatial frequency—HSF) scene of the other (i.e., low-pass city vs. high-pass highway or vice versa).

Cut-off frequencies for low- and high-pass image filters were obtained through pilot work making sure that the resulting hybrids did not produce any inherent biases towards a given end of the scale (i.e., non-sensitised observers reported seeing the LSF and HSF components of hybrids equally often). Observers completed one of two conditions in the experiment which used different stimulus display locations (see below). In one condition

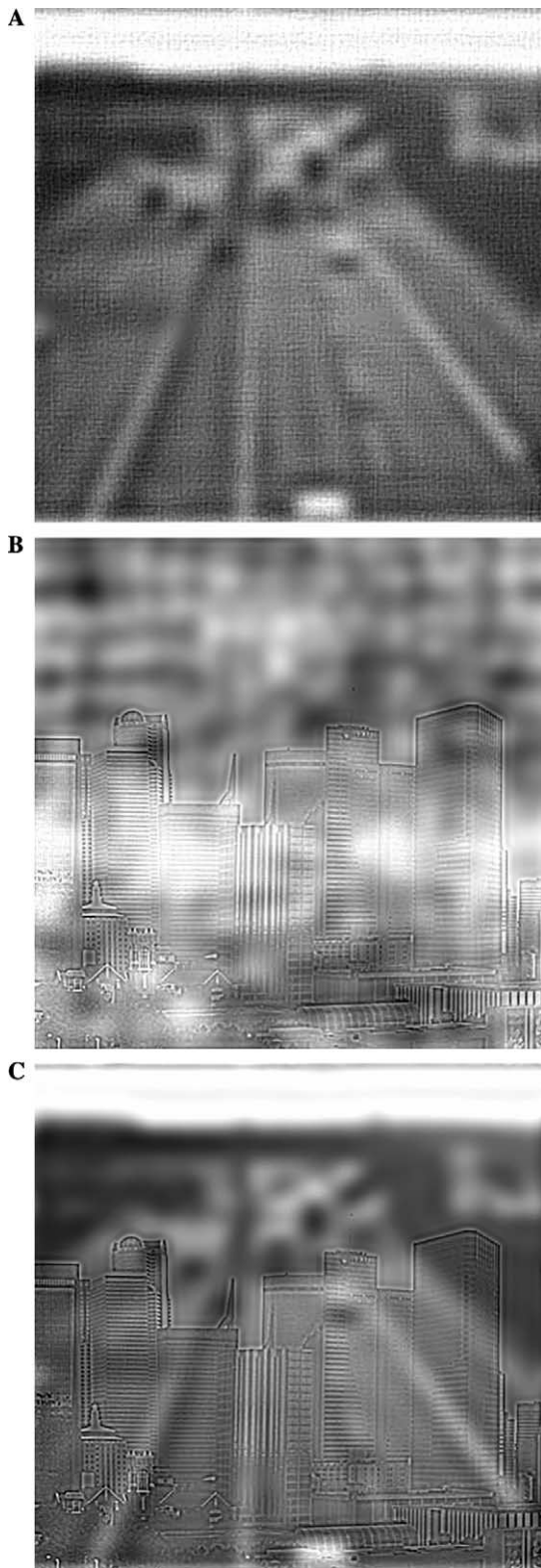


Fig. 1. Examples of stimuli used in the present study: (A) low-pass highway combined with high-pass structured noise; (B) high-pass city combined with low-pass structured noise; (C) a *hybrid*—low-pass highway combined with high-pass city.

(horizontal separation—HORS), stimuli were separated along the horizontal meridian and were displayed on either side of the vertical meridian. In the other condition (vertical separation—VERS), stimuli were separated along the vertical meridian, and presented in the upper- and lower-visual fields. Pilot work suggested that the use of slightly different filter cut-offs for the two conditions would be optimal. The cut-off frequencies for low- and high-pass filters for the HORS condition were 0.9 and 3.6 cycles/deg, and those for the VERS condition were 0.8 and 3.2 cycles/deg. For both sets of cut-offs, the low–high separation was two octaves thereby minimising any overlap of SF filter sensitivities (De Valois & De Valois, 1988).

Sixty-four images in each category were used to create sensitisation images and the remaining 16 were used to create hybrids. The combination of 64 scenes and 64 noise patterns for the sensitisation stimuli, and of 16 city and 16 highway images for the hybrids was randomised. Image filtering was carried out using a two-dimensional fast Fourier transform and a two-dimensional Butterworth filter. The resulting LSF and HSF images were added together to form either a sensitisation stimulus (scene + noise) or a hybrid (scene + scene).

Structured noise patterns were created also by using a fast Fourier transform in the following way. For each noise pattern, the SF spectrums of a city and a highway exemplar were computed. While all magnitude and orientation content was preserved, the phase information of each scene was randomly “shuffled” to an equal degree. The two “phase-shifted” images were then added together. The resulting noise pattern thus consisted of the same SF’s, at identical magnitude and orientations as those of the city and highway exemplars, but with random phase. This was done so that while no meaningful information was present in the noise patterns, due to the similarity of their SF content to those of the scene images, they should cause maximum interference to the relevant SF filters.

The stimuli were displayed on an EIZO FlexScan F980 CRT monitor driven by a Cambridge Research Systems 2/5 Visual Stimulus Generator, with a total display area subtending 20.7° (horizontal) by 15.5° (vertical) visual angle. Viewing distance was secured using a head and chin rest at 110 cm. Stimuli were displayed on a black background and measured $4.07^\circ \times 4.07^\circ$. In the HORS condition, stimuli appeared in either the left visual field or the right visual field. These two locations were centred vertically on the screen and were located 8.04° (centre of screen to centre of image) either side of the central fixation-cross (1°). In the VERS condition, stimuli were displayed either in the upper or the lower hemi-field, located 7.04° (centre to centre) below or above the fixation-cross, and centred horizontally.

2.1.3. Procedure

Observers were assigned to the HORS or VERS conditions. Further, within each condition, they were randomly assigned to one of two sensitisation regimes to counterbalance the particular scale to be sensitised in each hemi-field (HORS, LSF-left/HSF-right and vice versa; VERS, LSF-upper/HSF-lower, and vice versa). First, observers were shown full-bandwidth example scenes (a highway and a city), positioned on the display at locations relevant to each condition (left and right or upper and lower). They were instructed that they would be shown, very briefly, one image at a time in either one of these two positions, unpredictably. Their task was to report whether each image was of a highway or a city. It was explained to them that because of the spatial uncertainty, the optimal way of doing the task successfully was to look at the central fixation-cross, and use their peripheral vision to detect the images. Further, they were also warned that the images would be somewhat distorted. They were instructed that the experiment consisted of two parts: the first part was “for you to improve in this task and so you will receive feedback”; while in the second part there would be no feedback.

In the “sensitisation stage”, observers were shown “filtered-scene + noise” combinations in accordance with their sensitisation regime (LSF-scene + HSF-noise in one hemi-field and the reverse in the other, or vice versa). Trials were completed in blocks of 16. The maximum number of sensitisation trials that any observer had to complete was 256 (16 blocks). However, if an observer was able to complete two consecutive sensitisation blocks with only one error (or less) per block, then this stage was over for him or her. Each block of 16 trials consisted of 8 “LSF-scene + HSF-noise” and 8 “HSF-scene + LSF-noise” images, presented at the relevant locations. Of the eight images of each type, four contained a highway and four contained a city. In this stage, observers heard two distinct sounds to indicate a correct or incorrect response.

In the “test” stage observers continued viewing sensitisation stimuli but, unknown to the observer, test stimuli (“hybrids”) were randomly interleaved. There were 16 hybrids and 48 sensitisation stimuli in this stage. The scene–noise composition of the sensitisation stimuli was the same as in the sensitisation stage. Of the 16 hybrids, 8 were presented in each hemi-field, of which 4 consisted of an LSF highway and an HSF city and 4 consisted of the opposite. Observers continued reporting whether they perceived a highway or a city, only they no longer received feedback.

The trial sequence in both stages was as follows. The central fixation-cross appeared at the start of each trial. Observers were instructed to make sure of fixating the cross and then to press the space bar on the PC keyboard to start the trial. After 500 ms, the fixation-cross disappeared and the image was displayed for 125 ms in

one of the two possible locations (left or right hemi-field in the HORS condition; upper or lower hemi-field in the VERS condition). The observer’s response was followed by a feedback tone (only in the sensitisation stage) and the fixation-cross reappeared signalling the start of the next trial. The short (125 ms) stimulus duration was used to ensure that the retinal location of the stimuli was fixed from trial to trial, assuming correct fixation at stimulus onset.

The sensitisation stimuli used in the sensitisation stage were different from those used in the test stage. Each sensitisation scene was used a maximum of two times: once as an LSF and once as an HSF-scene (hence once in each hemi-field). Each hybrid in the test stage was shown only once. Observers recorded their responses by pressing one of two buttons on a game-pad, to indicate ‘highway’ or ‘city’. At the end of the experiment, observers were shown a hybrid and were debriefed. They were asked whether they had been explicitly aware of seeing both scenes at the same time during the experiment.

2.2. Results

For all analyses in the present study, we present the data for observers who reached a 70% accuracy level on the sensitisation trials (scene + noise), to ensure successful sensitisation. One observer in the HORS condition and four in the VERS condition failed to reach that criterion, leaving 9 and 12 successfully sensitised observers in the horizontal and vertical conditions, respectively.

2.2.1. Sensitisation stage

Seven of the 9 observers in the HORS condition, and 11 of the 12 observers in the VERS condition needed to complete all 16 blocks of the sensitisation stage. The remaining two in HORS needed only 11 and 4 blocks, respectively, and the remaining one in VERS needed 10 blocks to reach criterion. Fig. 2 shows blocked scene recognition performance summed across the two hemi-fields (hence across LSF and HSF scenes, which did not differ significantly— $F < 1$ in below ANOVA) for the sensitisation stage (the first 16 blocks), and for the sensitisation trials in the test stage (the last three blocks). It can be seen that performance improved across sensitisation trials in both conditions. An ANOVA with within-subjects factors *block* (19) and *scale* (2), and a between-subjects factor of *condition* (2) revealed a significant main effect of block; $F(8.605, 137.673) = 5.42$, $p < 0.0005$. As mentioned above, there was no effect of scale (LSF and HSF performances equal). No other effects were statistically significant; performance in the two conditions did not differ, and both groups showed a similar pattern of improvement across blocks of sensitisation.

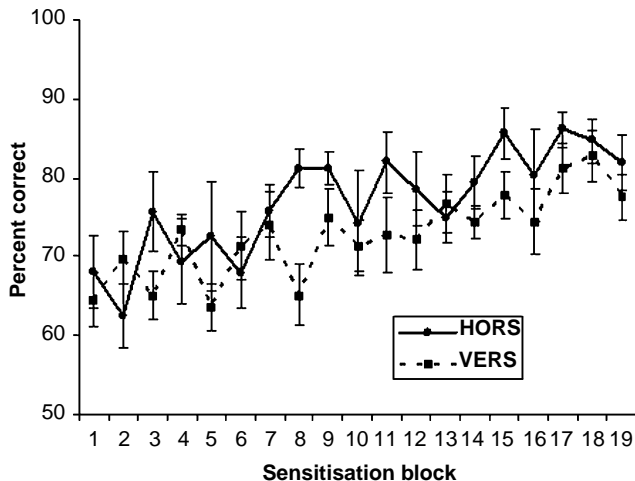


Fig. 2. Summary of sensitisation performance across the two conditions in Experiment 1: percent correct recognition of scenes (summed across hemi-fields—thus across LSF and HSF scenes), in blocks of 16 sensitisation trials, where the first 16 blocks (filled symbols) are for the sensitisation stage and the last 3 blocks (open symbols) are for the test stage. Error bars represent ± 1 standard error.

2.2.2. Test stage

Crucially, observers were shown hybrids (scene + scene) interleaved among the sensitisation trials (scene + noise) in the test stage. In the debrief phase none of our observers reported being aware of the hybrids; they consciously perceived only one scene at a time throughout. Fig. 3 shows average responses to hybrids

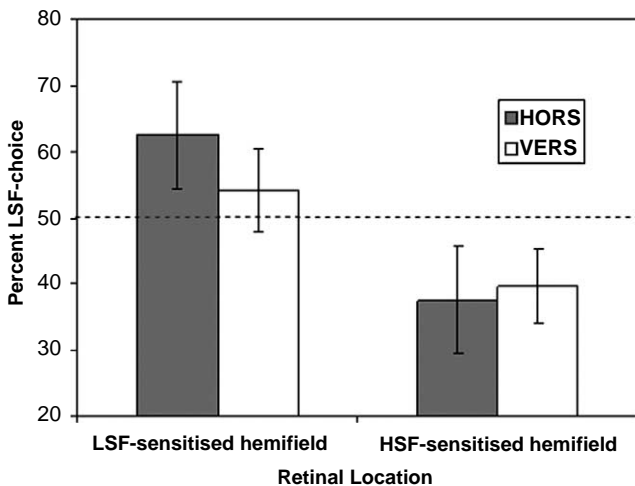


Fig. 3. Percentage of hybrid trials where the LSF component ($=100\% - \text{percent-HSF}$) was reported, across two hemi-fields sensitised to opposite spatial scale, for HORS and VERS conditions in Experiment 1. For half the sample in the HORS condition, left and right hemi-fields were sensitised to LSF and HSF scenes, respectively, while the opposite pattern was true for the rest. Similarly half the sample in the VERS condition were sensitised to LSF and HSF scenes in the upper and lower hemi-fields, respectively, while the rest were sensitised to the opposite pattern. The dashed line shows the 50% no-bias level, which would be expected if no sensitisation had occurred. Error bars represent ± 1 standard error.

presented in the LSF and HSF-sensitised hemi-fields. The measure we plot on the y-axis is the average percentage of trials where observers reported seeing the LSF component of a hybrid, since this is complementary to percent HSF choice ($\%HSF = 100 - \%LSF$). It can be seen that findings were similar in the HORS and VERS conditions ($F < 1$). In HORS observers showed a bias of 62.5% towards LSF in the LSF-sensitised field, while LSF choice dropped to 37.5% in the HSF-sensitised field (HSF bias = 62.5%); retinal-location-dependent bias varied perfectly symmetrically around 50%. Similarly, in VERS, the LSF bias was greater (54.17%) in the LSF-sensitised hemi-field and dropped in the HSF-sensitised hemi-field (39.58%, HSF bias = 60.42%). An ANOVA with the within-subjects factor *type-of-sensitisation* (LSF and HSF) and the between-subjects factor *condition* (HORS and VERS) revealed a significant main effect of *type-of-sensitisation* ($F(1, 19) = 12.30, p < 0.005$). There was no main effect of *condition* and no interaction between *condition* and *type-of-sensitisation* ($F < 1$). Observers reported the LSF component of a hybrid more frequently in the LSF-sensitised hemi-field than in the HSF-sensitised hemi-field; sensitisation to spatial scale was specific to visual field. This pattern did not differ across the horizontal and vertical separation conditions. LSF choice averaged across the two retinal locations was exactly 50% in HORS and close to 50% (46.88%) in VERS, indicating no inherent overall bias to either scale, and confirming the findings from our pilot cut-off estimation study (see stimuli).

2.3. Discussion

Experiment 1 provided evidence that not only can spatial scale processing of natural scenes be sensitised towards a particular scale, but also that such sensitisation can be retinal location specific. After being sensitised to opposite scales in two different retinal locations, observers perceived the same hybrid stimuli orthogonally (LSF vs. HSF) depending on to which location they were presented. Further, the finding that observers were unaware of the hybrid images suggests that attention channelled towards a particular scale at a particular retinal location might cause the observer to “lock on” to the sensitised component of a hybrid and miss the presence of the stimulus at the non-sensitised scale. Further, observers were never given any explicit information regarding the SF composition of the images. Indeed, they did not seem to be explicitly aware of the distinction between LSF and HSF images during the debrief phase—a direct question regarding this issue was asked later in Experiment 2.

Although we found clear evidence for specificity to retinal location across visual hemi-fields, the conclusions that can be drawn from these findings in relation to our

main claim (that flexible scale use involves early cortical sites) are limited. For instance, it is possible that observers sensitised entire hemi-fields to the relevant spatial scale rather than the precise locations of stimulus presentation within those hemi-fields. Such sensitisation could be accomplished at relatively late stages in the visual processing hierarchy where cells with large receptive field sizes are commonly found (cf. Kastner et al., 2001). Consequently, in Experiment 2 we sought to eliminate this possibility by sensitising the two quadrants of the visual field within each hemi-field to opposite scales.

3. Experiment 2

In this experiment, we intended to rule out the explanation that observers were simply sensitising entire hemi-fields to one spatial scale. We used the same design as that in the previous experiment but this time divided the display into four quadrants, and sensitised observers to separate spatial scales in the upper-left and lower-right vs. upper-right and lower-left quadrants. A further aim of this experiment was to measure the location specificity of sensitisation across smaller retinal distances. Thus, whereas in Experiment 1 the separations between the centres of images presented either side of the horizontal and vertical meridians were 16.07 and 14.07°, respectively, here we separated our stimuli by 7.7° horizontally, and 7.9° vertically (note that at this distance the separation of the inside edges was just 3.63° horizontally and 3.83° vertically). Research has established that receptive field (RF) sizes increase with the stage of visual processing (Kastner et al., 2001; Smith, Singh, Williams, & Greenlee, 2001). At an eccentricity of about 6° (retinal eccentricities in our Experiment 1 were 8.04° and 7.04° in the HORS and VERS conditions, respectively, and the eccentricity in this experiment was 5.6°), RF sizes in early macaque visual cortex range from about 0.5° in area V1 to about 6–7° in areas V3A and V4. Visual areas involved in later stages of processing such as area TE and TEO in the monkey and human temporal cortex have receptive field sizes that are larger than 7° (TEO) and typically as large as 26° in TE (Kastner et al., 2001). Thus, lack of transfer of sensitisation effects between the closer retinal locations used in this experiment would be consistent with the involvement of relatively early stages of visual processing prior to temporal cortex.

3.1. Method

3.1.1. Observers

Sixteen psychology undergraduates took part in the experiment. They all had normal or corrected to normal vision. They were paid a fee or offered course credits for their participation.

3.1.2. Stimuli and apparatus

Stimuli and apparatus were the same as those used in Experiment 1. The display was divided into four quadrants and the images could appear in any one of them. The diagonal distance between the centre of display and the nearest corner of stimuli in each quadrant was 2.7°. The horizontal distance between the upper-left and upper-right, and between the lower-left and lower-right quadrant stimuli (centre to centre) was 7.7°. The vertical distance between the upper and lower-left and between the upper and lower-right quadrant stimuli was 7.9° (centre to centre). Note that these distances were just 3.6° and 3.8°, respectively, between the inside edges of the stimuli. Optimal filter cut-offs for the new eccentricities were once again estimated through pilot work; low- and high-pass cut-offs used were 0.75 and 3 cycles/deg, respectively.

3.1.3. Procedure

Observers were randomly allocated into two sensitisation patterns: LSF sensitisation in the upper-left and lower-right quadrants and HSF sensitisation in the upper-right and lower-left quadrants, or the opposite. Trial and stimulus numbers for each quadrant was half that for a given hemi-field in Experiment 1, adding to the same total for each type of sensitisation field (LSF vs. HSF). Pilot work suggested that sensitisation in this four-quadrant task can be less efficient due to the increased difficulty involved. Therefore, we used a 2-consecutive-day training regime in this experiment. On the first day, observers completed 16 blocks of sensitisation trials, exactly as in the sensitisation stage of Experiment 1. On the second day, they did the same followed immediately by a test stage, again identical to that in Experiment 1 except for the quadrant display. In the debrief phase, in addition to being asked whether they were aware of the two-scene hybrids, observers were told about coarse and fine images and how they were distributed across the quadrants during sensitisation, and asked if they were aware of this.

3.2. Results

Three of our 16 observers failed to reach the successful sensitisation criterion of 70% accuracy in the test block and were excluded from the following analyses. All observers needed to complete all 16 blocks of sensitisation trials on the first day, and all but one of the observers completed all 16 of the sensitisation stage blocks on the second day (the remaining observer needed 13 blocks to reach criterion). Fig. 4 shows blocked scene recognition performance summed across the four quadrants (hence across LSF and HSF scenes, which did not differ significantly— $F < 1$ in below ANOVA). The total number of sensitisation blocks that were completed by the observers over the 2 days was 35 (32

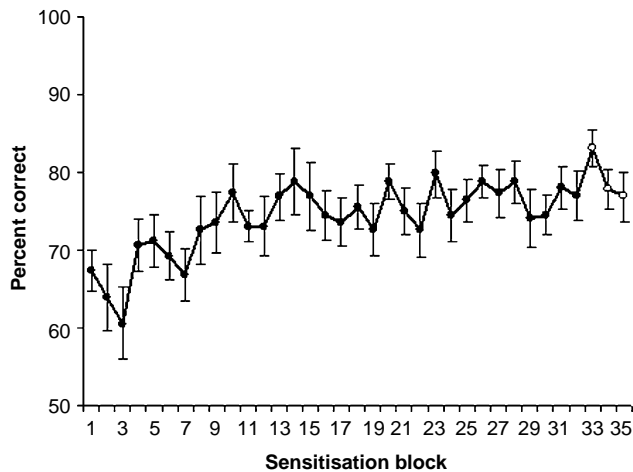


Fig. 4. Summary of sensitisation performance in Experiment 2: percent correct recognition of scenes (summed across the four quadrants—thus across LSF and HSF scenes), in blocks of 16 sensitisation trials, where the first 32 blocks (filled symbols) are for the sensitisation stage and the last 3 blocks (open symbols) are for the test stage. Error bars represent ± 1 standard error.

sensitisation stage blocks, and three sensitisation blocks in the test stage), and observers showed a significant improvement across these blocks ($F(7.995, 87.944) = 2.45$, $p < 0.05$).

In this experiment observers were sensitised to each scale in two different locations. So, for example, a given observer might be sensitised to LSF scenes in the upper-left and lower-right quadrants. Thus, for the responses to the hybrid stimuli, we first looked to see if there were any differences between the two locations for each scale, and found no differential effects across locations within each type of SF ($p > 0.7$ for both SF's). Therefore, in subsequent analyses, we combine responses across the two locations used for each scale. As in the previous experiment, none of the observers reported seeing a hybrid stimulus at any point. In addition, they indicated that they were unaware of the coarse-fine distinction and which quadrants each type of image could appear in during the experiment.

The findings in this experiment were similar to those in Experiment 1. Fig. 5 shows average percent LSF choice in the LSF and HSF-sensitised fields. It can be seen that once again, LSF bias was higher (56.73%) in the LSF quadrants and dropped (38.46% – HSF bias = 61.54%) in the HSF quadrants. This difference in LSF bias between the LSF and HSF-sensitised quadrants was statistically significant; $t(12) = 2.50$, $p < 0.05$. To express this in another way, the combination of LSF bias in the LSF quadrants and HSF bias in the HSF quadrants (i.e., the percentage of with-prediction responses) was 59.13%. The average LSF bias across all fields was 47.6% (not different from 50%; $p = 0.7$) indicating once again, no overall bias towards a particular scale.

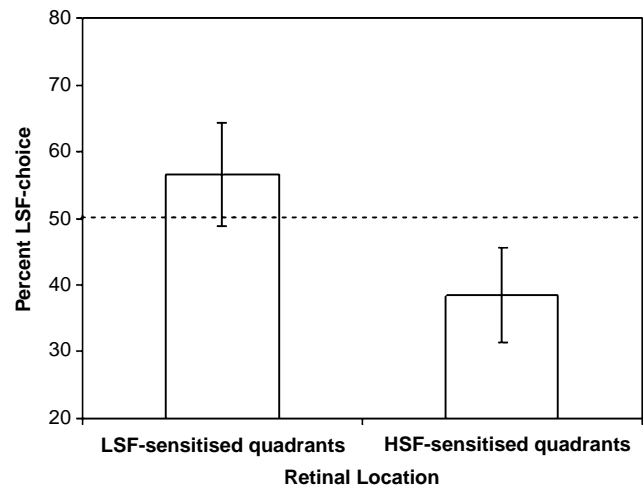


Fig. 5. Percent LSF choice ($100\% - \%HSF$) on hybrid trials across four retinal locations in Experiment 2. Upper-left + lower-right quadrants and upper-right + lower-left quadrants were sensitised to LSF and HSF scenes, respectively, for half the sample, while the opposite pattern was true for the rest. The dashed line shows the 50% no-bias level, which would be expected if no sensitisation had occurred. Error bars represent ± 1 standard error.

3.3. Discussion

Experiment 2 provided further support for retinotopic specificity of sensitisation to spatial scale. Crucially, we found evidence for retinotopic mapping at a finer resolution than in Experiment 1; sensitisation to a particular spatial scale was specific to a given quadrant of the display, where the horizontal and vertical centre-to-centre distance between the stimulus locations was 7.7° and 7.9° (3.6° and 3.8° inside edge to inside edge), respectively. As mentioned above, RF sizes in the monkey visual cortex increase with level of visual processing; ranging from about 0.5° in V1 to about $6\text{--}7^\circ$ in V4 and V3A, and increases substantially at later stages such as TEO and TE to as much as 26° . The level of retinotopic specificity we report here suggests therefore that such late stages may not be involved.

None of our observers reported being aware of the hybrid stimuli. Further, observers stated that they were not explicitly aware that some scenes were coarse and some fine, and that this determined where on the screen they were presented. However, despite our observers' assertions, there is the possibility that a response bias could explain the findings from Experiments 1 and 2. After the long run of sensitisation trials, observers may at some level have perceived both components of a hybrid, but have been biased toward reporting the sensitised component of the hybrid because that is what they had been trained to do. Consequently, in Experiment 3, we sought to rule out this explanation using 'incongruent' single-scene plus noise stimuli instead of hybrids in the test stage. These incongruent

images were orthogonal to the observers' sensitisation pattern; the scene component of the image was presented at the scale orthogonal to the sensitised scale and the noise component was presented at the sensitised scale. If a response bias is responsible for hybrid performance in Experiments 1 and 2, then for these incongruent trials we should expect to find that observers are equally able to categorise the scenes present in the non-sensitised SF's.

4. Experiment 3

As in Experiment 2, we sensitised observers to a particular SF depending on the quadrant of presentation using the same scene + noise stimuli, and they were then tested across 64 trials (test stage) without feedback. However, whilst hybrids were used in the test stage of Experiment 2, here we randomly interleaved single-scene incongruent trials where the SF of the scene component was orthogonal to the observers' sensitisation (at each particular quadrant of presentation). Where observers were sensitised to HSF-scene + LSF-noise images (or LSF-scene + HSF-noise images), the incongruent trials were LSF-scene + HSF-noise images (or HSF-scene + LSF-noise images).

We predicted that scene categorisation performance would be worse for incongruent trials than for the sensitisation trials of the test stage (hereafter referred to as congruent trials). If observers are sensitised to a particular SF at a particular location, such sensitisation will drive observers to attend to the sensitised component of an incongruent image, which would be the noise component. Perceiving the noise component would reduce performance since there is no scene information present here. Such a performance decrement would suggest that a response bias cannot account for the findings in Experiments 1 and 2. However, there is the possibility that on finding no valid scene information at that scale, observers may be forced to switch to attending to the non-sensitised component of the image. This would be available in "iconic memory" and may bring performance on incongruent trials up to the same level as congruent trial performance, concealing the effect of retinotopic sensitisation to spatial scale. Thus, backward masking with noise was used in the test stage, to prevent such immediate retrieval of the scale-incongruent scene.

4.1. Method

4.1.1. Observers

Thirty-four University of Surrey students took part in the experiment. They all had normal or corrected to normal vision. They were paid a fee or offered course credits for their participation.

4.1.2. Stimuli and apparatus

Stimuli and apparatus were the same as those used in Experiment 2. The screen was divided into four quadrants and the images could appear in any one of them. The distances between the quadrants were identical to those in Experiment 2. For the noise masks, 80 structured noise patterns were created as described in the method of Experiment 1.

4.1.3. Procedure

As in Experiment 2, observers were randomly assigned to one of two sensitisation patterns: LSF sensitisation in the upper-left and lower-right quadrants and HSF sensitisation in the upper-right and lower-left quadrants, or the opposite. Like Experiment 2, on both days observers completed a maximum of 16 blocks of sensitisation trials, and on day two this was immediately followed by the test stage. The test stage consisted of four blocks, each block containing 12 sensitisation trials and 4 test trials. Observers were not informed that there were two different kinds of trials in the test stage. Like Experiments 1 and 2, there were four types of image (HSF city, HSF highway, LSF city, and LSF highway). For each block, three sensitisation trials and one test trial were presented in each quadrant, the scale of which corresponded to the observer's sensitisation pattern. Across the four blocks, equal numbers of highways and cities were presented in each quadrant. All trials in the test stage were backward masked by, randomly selected, structured noise patterns. Thus, for each trial in the test stage one image was presented in one of the four quadrants for 125 ms, and then a randomly selected noise mask was displayed in this same location, disappearing once the observer had made their response.

4.2. Results

Sixteen of our 34 observers failed to reach the successful sensitisation criterion of 70% accuracy in the test stage and were excluded from the following analyses.

4.2.1. Sensitisation stage

Of the remaining 18 observers, all but one needed to complete all 16 blocks of sensitisation trials on the first day (one observer completing 12 blocks) and all observers completed all 16 sensitisation stage blocks on the second day. Fig. 6 shows blocked scene recognition performance summed across the four quadrants (hence across LSF and HSF scenes, which did not differ significantly— $F < 1$ in below ANOVA). The total number of sensitisation stage blocks that were completed by the observers over the 2 days was 36 (32 in the sensitisation stages and 4 in the test stage) and it can be seen that performance improved throughout the sensitisation and test stages. An ANOVA with within-subjects factors of *block* (36) and *scale* (2) revealed a significant main effect

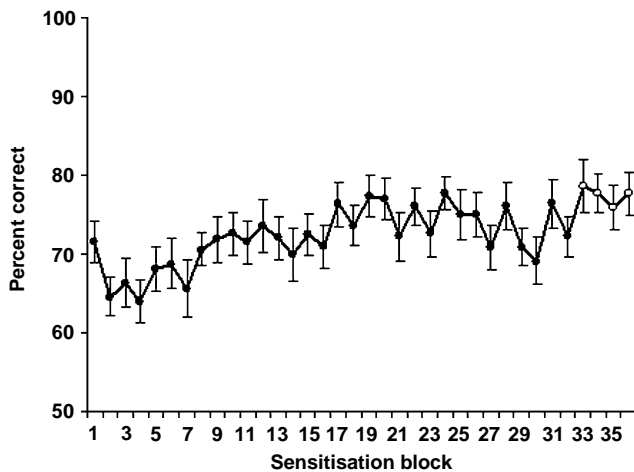


Fig. 6. Summary of sensitisation performance in Experiment 3: percent correct recognition of scenes (summed across the four quadrants—thus across LSF and HSF scenes), in blocks of 16 sensitisation trials, where the first 32 blocks (filled symbols) are for the sensitisation stage and the last 4 blocks (open symbols) are for the test stage. Error bars represent ± 1 standard error.

of block; $F(10.843, 173.481) = 2.27$, $p < 0.05$. No other effects were statistically significant.

4.2.2. Test stage

As in Experiment 2, observers were sensitised to not only two different scales but were also sensitised to each of these scales in two different locations. We first looked to see if there were any differences between the two locations for each scale for both congruent and incongruent trials, and found no differential effects across the locations for each type of SF for both trial types ($p > 0.1$ for both SF's in congruent trials; $p > 0.3$ for both SF's in incongruent trials). Thus, we combined responses across locations for each scale for both trial types. We then looked to see if there were any differences between the scales for both trial types. For both congruent trials ($t(17) = -0.546$, $p > 0.5$) and the incongruent trials ($t(17) = 0.108$, $p > 0.9$) there were no differences between LSF and HSF trials. Therefore, we also combine responses across the two scales for both trial types.

Combining responses across location and scale for both trial types allowed us to compare the total number of correct scene categorisation responses for the congruent trials ($M = 77.55\%$, $SE = 2.82$) to that of the incongruent trials ($M = 72.57\%$, $SE = 1.15$). We found that congruent trials performance was significantly better than incongruent trial performance; $t(17) = -1.903$, $p < 0.05$.

4.3. Discussion

The results from Experiment 3 show that observers were more accurate in recognising the test stage images when the spatial scale of the scene matched the scale of

the scenes presented in that location during sensitisation (congruent trials) than when the scene was of the orthogonal scale (incongruent trials). The reduction in recognition performance for incongruent trials provides further evidence that spatial scale processing of scenes can be sensitised towards a particular scale. Furthermore, the results imply that sensitisation is retinal location specific. The reduced performance in incongruent trials meant that sensitisation did not transfer to alternative locations. For instance, observers sensitised to LSF scenes in the upper-left quadrants were better at recognising the LSF scenes than HSF scenes in this location, despite being sensitised to HSF scenes in the adjacent upper-right and lower-left quadrants. Most importantly, these results suggest that the findings in Experiments 1 and 2 could not be explained purely in terms of a response bias. The enhancement in recognition on the congruent trials as compared to the incongruent trials in Experiment 3 is difficult to attribute to a response bias because valid scene information is never presented at both scales.

5. General discussion

In three experiments, we investigated whether flexible scale use as a result of sensitisation is specific to retinal location. We sensitised observers to a particular band of SF's by presenting them with a stream of either low- or high-pass filtered scenes (combined with structured noise at the unoccupied SF's) at different locations in the visual field, and asked them to categorise the scenes as "city" or "highway". In Experiments 1 and 2, we then interleaved hybrid stimuli (both a city and a highway with opposite SF content) in amongst the sensitisation images, at all retinal locations. The category of the scene that an observer reported on a hybrid trial at a given location indicated his/her SF bias at that location. We found that not only did observers sensitise to a particular scale at a given location, but also that this sensitisation did not transfer to an alternative location. However, there was the possibility that a response bias could explain the performance on the hybrid trials; participants might have perceived both components but reported the appropriate SF component of the hybrid because that was what they were trained to do during sensitisation. In Experiment 3, we explored this issue by replacing hybrids with incongruent scene plus noise stimuli. The SF's of the scenes in these incongruent trials were orthogonal to the SF's of the scenes observers had been sensitised to. We found that categorisation performance on these incongruent trials dropped below performance on congruent (sensitisation) trials. Observers were sensitised to expect scenes in a certain SF band in each location and performance suffered on incongruent trials because the meaningful scenes were not present at the

expected SF's. Therefore, a response bias explanation does not account for the hybrid performance in Experiments 1 and 2 since Experiment 3 suggests that sensitisation actually influences the perception of the SF filtered images.

The retinotopic specificity of sensitisation was found across both large (14.07° and 16.07°) and relatively small (7.7° and 7.9°) areas in the visual field. It is important to note however that as mentioned earlier, the separations were smaller between the inside edges of the stimuli (10° and 12° in Experiment 1, and 3.6° and 3.8° in Experiment 2). It is possible to argue therefore that the specificity of sensitisation effects might be even higher than our conservative image-centre to centre separation figures suggest. For instance, it is possible that cells with receptive fields as small as 4° or 5° would cover the inside edge of both images. If the output of such cells were used then we should expect a failure of location-specific sensitisation. However, this has not been observed here suggesting such cells did not mediate responses and therefore implying earlier stages of processing where receptive fields are less than $4\text{--}5^\circ$ may be involved in the location-specific sensitisation observed here.

Our findings suggest the involvement of relatively early stages of visual processing in effects of spatial scale sensitisation. Lack of transfer across a relatively small distance in the visual field suggests that late stages of the visual hierarchy where RF sizes exceed this distance are not involved (Smith et al., 2001; Kastner et al., 2001—but see Dill, 2002 for caution). This is consistent with our argument: flexible use of spatial scale found in the perception of hybrid faces and scenes, either as a function of categorisation (Schyns & Oliva, 1999; Schyns et al., 2002) or sensitisation (Oliva & Schyns, 1997) may involve attentional modulation of early SF channels. Our investigation is not sufficient to conclusively point to V1 specifically, where the resolution of retinotopic mapping is far finer than we tested here. (Using very small separations is problematic; our relatively large stimulus size, required for successful recognition, means that testing specificity at such fine resolutions is only possible with considerable image overlap.) However, we believe the evidence presented here suggests at least that the locus of these phenomena is not at a late stage in the visual processing hierarchy.

5.1. Review of the attentional modulation account and findings so far

Let us review this attentional modulation account of effects involving flexible scale use in the light of these findings. We argue that diagnosticity can act as an attentional filter in the processing of SF information. Particular types of spatial scale information can be diagnostic for a given type of face categorisation (Schyns & Oliva,

1999) even at a specific location within the face stimuli (Schyns et al., 2002), or according to what scale meaningful information is restricted to (Oliva & Schyns, 1997), again at a given retinal location (the present study). A similar process of diagnosticity can also be found in the psychophysical uncertainty paradigm; uncertainty about the SF of a sinusoidal grating elevates contrast threshold for detection (Davis et al., 1983; Sowden et al., 2003). For each trial during a block of gratings varying in SF, the diagnostic information is the specific SF of the grating presented on that trial. Crucially, a sound cue indicating the diagnostic scale, makes detection more likely. Similarly, using SF filtered scene plus noise stimuli, sound cues direct attention toward the diagnostic scale (the SF of the scene component) enhancing scene detection (Özgen et al., 2005). In all these cases, it is essential to be attending to a particular scale, sometimes at a particular spatial location, in order to accomplish the task. Thus diagnosticity necessitates attention to these parameters. Evidence suggests that attentional modulation of SF channel processing at early stages of visual analysis may indeed be possible; (top-down) attention to the SF of a grating (through the use of symbolic cues) does not transfer far beyond a two-octave range of SF's, suggesting SF tuning such as that typical of early cortical SF channels (Sowden et al., 2003). Task or categorisation-based diagnosticity in the perception of complex patterns might thus drive attention to a particular band of SF's, modulating the activity of SF channels in a similar fashion.

6. Conclusions

The evidence presented here is consistent with attentional modulation of spatial frequency processing. Flexible scale use, resulting from sensitisation, is retinal location specific at relatively fine resolutions. The SF tuning of attentional modulation effects in grating detection, and the retinotopic specificity of scale sensitisation effects reported here, both imply a relatively early stage of visual analysis, perhaps as early as V1.

Acknowledgments

This work was supported by BBSRC Grant Nos. S13185 and S13186 awarded to Paul Sowden and Philippe Schyns.

References

- Ahissar, M., & Hochstein, S. (1996). Learning pop-out detection: Specificities to stimulus characteristics. *Vision Research*, 36, 3487–3500.

- Ahissar, M., & Hochstein, S. (1997). Task difficulty and the specificity of perceptual learning. *Nature*, *387*, 401–406.
- Barrett, D. J. K., Bradshaw, M. F., Rose, D., Everatt, J., & Simpson, P. J. (2001). Reflexive shifts of covert attention operate in an egocentric coordinate frame. *Perception*, *30*, 1083–1091.
- Bashinski, H. S., & Bacharach, V. R. (1980). Enhancement of perceptual sensitivity as the result of selectively attending to spatial locations. *Perception & Psychophysics*, *28*, 241–248.
- Bonnar, L., Gosselin, F., & Schyns, P. G. (2002). Understanding Dali's slave market with the disappearing bust of voltaire: A case study in the scale information driving perception. *Perception*, *31*, 683–691.
- Davis, E. T., & Graham, N. (1981). Spatial frequency uncertainty effects in the detection of sinusoidal gratings. *Vision Research*, *21*, 705–712.
- Davis, E. T., Kramer, P., & Graham, N. (1983). Uncertainty about spatial frequency, spatial position, or contrast of visual patterns. *Perception & Psychophysics*, *33*, 20–28.
- De Valois, R. L., & De Valois, K. K. (1988). *Spatial vision*. Oxford, UK: Oxford University Press.
- Dill, M. (2002). Specificity versus invariance of perceptual learning: The example of position. In M. Fahle & T. Poggio (Eds.), *Perceptual learning* (pp. 219–231). Cambridge, Massachusetts, USA: The MIT Press.
- Eckstein, M. P., Shimozaki, S. S., & Abbey, C. K. (2002). The footprints of visual attention in the Posner cueing paradigm revealed by classification images. *Journal of Vision*, *2*, 25–45.
- Eriksen, C. W., & Hoffman, J. E. (1972). Temporal and spatial characteristics of selective coding from visual displays. *Perception & Psychophysics*, *12*, 210–294.
- Fahle, M., Edelman, S., & Poggio, T. (1995). Fast perceptual learning in hyperacuity. *Vision Research*, *35*, 3003–3013.
- Gandhi, S. P., Heeger, D. J., & Boynton, G. M. (1999). Spatial attention affects brain activity in human primary visual cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *96*, 3314–3319.
- Hawkins, H. L., Hillyard, S. A., Luck, S. J., Mouloua, M., Downing, C. J., & Woodward, D. P. (1990). Visual attention modulates signal detectability. *Journal of Experimental Psychology: Human Perception and Performance*, *16*, 802–811.
- Hübner, R. (1996a). The efficiency of different cue types for reducing spatial-frequency uncertainty. *Vision Research*, *36*, 401–408.
- Hübner, R. (1996b). Specific effects of spatial-frequency uncertainty and different cue types on contrast detection: Data and models. *Vision Research*, *36*, 3429–3439.
- Kastner, S., Weerd, P. D., Pinsk, M. A., Elizondo, M. I., Desimone, R., & Ungerleider, L. G. (2001). Modulation of sensory suppression: Implications for receptive field sizes in human visual cortex. *Journal of Neurophysiology*, *86*, 1398–1411.
- LaBerge, D. (1983). Spatial extent of attention to letters and words. *Journal of Experimental Psychology: Human Perception and Performance*, *9*, 371–379.
- Luck, S. J. (1998). Neurophysiology of selective attention. In H. Pashler (Ed.), *Attention* (pp. 257–295). Hove, East Sussex, UK: Psychology Press Ltd.
- Martinez, A., DiRusso, F., Anllo-Vento, L., Sereno, M. I., Buxton, R. B., & Hillyard, S. A. (2001). Putting spatial attention on the map: Timing and localization of stimulus selection processes in striate and extrastriate visual areas. *Vision Research*, *41*, 1437–1457.
- Motter, B. C. (1993). Focal attention produces spatially selective processing in visual cortical areas V1, V2, and V4 in the presence of competing stimuli. *Journal of Neurophysiology*, *70*, 909–919.
- Oliva, A., & Schyns, P. G. (1997). Coarse blobs or fine edges. Evidence that information diagnosticity changes the perception of complex visual stimuli. *Cognitive Psychology*, *34*, 72–107.
- Özgen, E., Sowden, P. T., Schyns, P. G., & Daoutis, C. (2005). Top-down attentional modulation of spatial frequency processing in scene perception. *Visual Cognition*, *12*(6), 925–937.
- Posner, M. I. (1980). Orienting of attention. *The Quarterly Journal of Experimental Psychology*, *32*, 3–25.
- Posner, M. I., & Gilbert, C. D. (1999). Attention and primary visual cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *96*, 2585–2587.
- Schyns, P. G., & Oliva, A. (1999). Dr. Angry and Mr. Smile: When categorization flexibly modifies the perception of faces in rapid visual presentations. *Cognition*, *69*, 243–265.
- Schyns, P. G., Bonnar, L., & Gosselin, F. (2002). Show me the features! Understanding recognition from the use of visual information. *Psychological Science*, *13*, 402–409.
- Sengpiel, F., & Hübner, M. (1999). Visual attention: Spotlight on the primary visual cortex. *Current Biology*, *9*, 318–321.
- Shiu, L., & Pashler, H. (1995). Spatial attention and vernier acuity. *Vision Research*, *35*, 337–343.
- Smith, A. T., Singh, K. D., Williams, A. L., & Greenlee, M. W. (2001). Estimating receptive field size from fMRI data in human striate and extrastriate visual cortex. *Cerebral Cortex*, *11*, 1182–1190.
- Somers, D. C., Dale, A. M., Seiffert, A. E., & Tootell, R. B. H. (1999). Functional MRI reveals spatially specific attentional modulation in human primary visual cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *96*, 1663–1668.
- Sowden, P. T., Özgen, E., Schyns, P. G., & Daoutis, C. (2003). Expectancy effects on spatial frequency processing. *Vision Research*, *43*, 2759–2772.
- Sowden, P. T., Rose, D., & Davies, I. R. L. (2002). Perceptual learning of luminance contrast detection: Specific for spatial frequency and retinal location but not orientation. *Vision Research*, *42*, 1249–1258.
- Tootell, R. B. H., Silverman, M. S., Switkes, E., & De Valois, R. L. (1982). Deoxyglucose analysis of retinotopic organization in primate striate cortex. *Science*, *218*, 902–904.
- Tootell, R. B. H., Hadjikhani, N., Hall, E. K., Marrett, S., Vanduffel, W., Vaughan, J. T., & Dale, A. M. (1998). The retinotopy of visual spatial attention. *Neuron*, *21*, 1409–1422.
- Yantis, S., & Johnston, J. C. (1990). On the locus of visual selection: Evidence from focused attention tasks. *Journal of Experimental Psychology: Human Perception and Performance*, *16*, 135–149.
- Yantis, S. (1998). Control of visual attention. In H. Pashler (Ed.), *Attention* (pp. 223–256). Hove, East Sussex, UK: Psychology Press Ltd.
- Yeshurun, Y., & Carrasco, M. (1999). Spatial attention improves performance in spatial resolution tasks. *Vision Research*, *39*, 293–306.